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The “Foliage Is the Fruit” Hypothesis: Complex Adaptations in Buffalograss (*Buchloe dactyloides*)

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ABSTRACT.—Buffalograss (*Buchloe dactyloides*) has been described as an excellent fit for Janzen’s “Foliage is the Fruit” (FF) hypothesis, which suggests that large grazing animals ingest and later disperse seeds of some herbs when consuming their foliage. We tested this hypothesis by feeding buffalograss burs and legume seeds to ruminally fistulated beef steers. Our objectives were to determine (1) rumen residence times of buffalograss burs, free buffalograss caryopses and legume seeds; (2) total tract residence times for the three types of propagules; (3) percentage propagule survival after passage and (4) germinability of fed and unfed burs and caryopses. Bur survival (3%) and germination percentage were lower than previously reported, but this can be explained by differences in feeding and germination procedures. Significant numbers of free caryopses recovered from the feces also germinated. Previously undescribed hairs on the burs’ awn-like projections delayed passage through the animals and assured that many burs were broken during rumination. We concur that buffalograss is an excellent fit for the FF hypothesis, but our results and observations suggest that the buffalograss/grazing-animal interaction is more complex than it initially appeared.

INTRODUCTION

The Foliage is the Fruit (FF) hypothesis proposes that large herbivores inadvertently ingest seeds when consuming foliage of some herbaceous plants (Janzen, 1984). The plant pays a cost in lost tissue, but benefits because the animals disperse viable seed farther than possible by passive means. Buffalograss (*Buchloe dactyloides*), with its seeds positioned within foliage, has been proposed as a grass with most of the FF traits (Quinn *et al.*, 1994). These workers argued that the ability of buffalograss to disseminate endozoochorically is responsible for its spread from a presumed origin in Mexico across the central United States to southern Canada. Buffalograss’ wide range is in contrast to the restricted ranges of five closely related monospecific genera without FF traits.

Quinn *et al.* (1994) reported that survival of buffalograss diaspores (hereafter referred to as “burs”) is high following passage through cattle (*Bos taurus*). They noted that some burs were broken during passage, but did not account for any caryopses released from the burs, nor did they provide a numerical estimate of burs surviving passage. Our earlier research indicated that recovery of burs from feces of domestic cattle fed burs and hay was low, but a substantial number of caryopses were present. A very high percentage of the burs apparently disintegrated because of remastication, releasing the caryopses, which were digested or passed in the feces.

Other herbaceous species exhibit varying levels of viability after ruminant digestion. Ocumpaugh *et al.* (1993) reported germination of ca. 90% for switchgrass (*Panicum virgatum*) seed recovered from the feces 12 h after feeding to cattle, but germination fell to less than 10% for seed recovered 96 h after feeding. Burton and Andrews (1948) reported uniformly high germination for bermudagrass (*Cynodon dactylon*) across 10 days of recov-

ery, but levels fell to near zero for several other tropical grass species. Several forbs also germinate in significant numbers after bovine digestion, including common lespedeza (*Lespedeza striata*) (Burton and Andrews, 1948). Simao Neto *et al.* (1987) reported significant germination for several tropical and subtropical legumes fed to cattle, domestic sheep (*Ovis aries*) and domestic goats (*Capra hircus*). In addition, there are numerous references in the literature to viable herbaceous seeds found in the feces of free-ranging ruminants (Ridley, 1930; Harmon and Keim, 1934; Dore and Raymond, 1942; Wicklow and Zak, 1983).

Germination of intact buffalograss burs is typically low and slow (Wenger, 1941; Fry *et al.*, 1993). Burs from commercial seed producers usually are "primed" by the "Hays treatment." This involves soaking the burs for 24 h in a 0.5% KNO₃ solution, followed by wet chilling for 6 wk at 5 C, then drying at <49 C (Wenger, 1941). The Hays treatment usually increases germination from about 10% to 70%. Ahring and Todd (1977) extracted an unknown oil from the thickened glumes in which the buffalograss caryopses are contained. They suggested the oil simply waterproofs the burs and largely accounts for the typically low germination of non Hays-primed buffalograss seed. If so, this would be functionally comparable to coat-imposed dormancy due to interference with water uptake (Bewley and Black, 1994), commonly referred to as "hard seed." Ahring and Todd (1977), however, did not rule out the possibility of other unknown germination inhibitors. They also showed that free caryopses have higher germination than chemically treated or untreated intact burs. Other workers have reported improved germination of buffalograss burs following soaking in tap water (Wenger, 1941; Fry *et al.*, 1993). Svoboda (1991) also reported enhanced germination of free caryopses compared to intact burs both with and without the Hays treatment.

A thorough understanding of ruminant digestion is necessary both to design useful seed-feeding experiments and to interpret results. Ruminant digestion is the most complicated among mammals from physiological, microbial, structural and motility standpoints (Church, 1988; Van Soest, 1994). Its central features, allowing for digestion of high-fiber diets, are the unique four-chambered stomach and rumination. The first two stomach chambers, jointly termed the reticulorumen, are the primary site of microbial digestion of fibrous feeds. Regurgitation and remastication (*i.e.*, rumination) of previously ingested feed are necessary to reduce particle size and enhance microbial fermentation. There are considerable digestive differences among species of ruminants, especially related to body size (Hofmann, 1988). Smaller ruminants tend to be concentrate feeders that select small plant parts high in easily digested cell contents and lower in cell-wall fiber. In concentrate feeders, passage rates are relatively fast, and the importance of fermentation and rumination is less. Large ruminants, including cattle and bison (*Bison bison*), tend to be less discriminating grazers and consume mostly grasses. Their energy requirements per unit of body weight are less than those of small ruminants, which makes exploitation of a fibrous grass diet possible. Passage rates are slower, and fermentation and rumination are important to reduce particle size and release energy from cell-wall components, principally cellulose and hemicellulose.

Age and size of individual animals can influence digestion within a species (Lyford, 1988). Smaller, younger individuals typically achieve less efficient fiber digestion and faster passage than larger animals consuming the same fibrous ration. Forage quality and physical structure also affect passage rates. Passage rate accelerates with increased feed digestibility and decreased initial particle size, as with ground feeds. These factors also reduce time and extent of rumination.

Grazers typically consume a few large meals per day, the food being swallowed quickly with minimum mastication (Hofmann, 1988). Small, dense objects in the forage, such as typical seeds, tend to settle to the bottom of the rumen cranial sac. Ruminal contractions

soon move them to the reticulum where they are entrapped by the reticulorumenal fold and transferred to the omasum, or third stomach chamber. Coarse fiber particles initially have a specific gravity less than 1.0 and collect in a floating rumen raft, which is stratified by size and density of particles. The presence of coarse fiber particles in the rumen stimulates rumination, during which particles are regurgitated, remasticated and reswallowed. Particles over time become smaller due to mechanical breakdown and denser due to digestion of lighter cell-wall components. The smaller, denser particles eventually settle out of the raft and leave the reticulorumen. Although larger particles can leave the reticulorumen, in cattle most particles are reduced to 4 mm or less before passage.

The objectives of our study were to determine (1) rumen digesta raft concentrations of buffalograss burs and caryopses and legume seeds as an indication of their rumen residence times; (2) fecal concentrations of burs, caryopses and legume seeds as an indication of their total gastrointestinal tract residence times; (3) total passage of burs, caryopses, and legume seeds, and (4) germination of animal-treated burs and caryopses compared with that of untreated burs and caryopses.

MATERIALS AND METHODS

Three experiments were conducted at the University of Nebraska-Lincoln Department of Animal Science ruminant nutrition facility. The experimental steers were housed indoors in individual pens under thermoneutral environmental conditions. The steers were fed a high-quality ground (2 cm) alfalfa (*Medicago sativa*) hay diet before and during each of three experiments. *In vitro* dry matter disappearance digestibility of the hay was 60% and the protein content was 18%. In each experiment, ca. 30,000 intact buffalograss burs and 30,000 legume seeds were fed to each of three ruminally fistulated mixed-breed beef steers.

Legume seeds were fed to compare passage dynamics of buffalograss with a more typical seed form. The legume species were canadian tickclover (*Desmodium canadense*) in experiments 1 and 2, and Illinois bundleflower (*Desmanthus illinoensis*) in experiment 3. Seeds of the two legume species were similar in size, shape and weight, 0.49 g/100 seeds vs. 0.61 g/100 seeds, respectively, compared with about 1.37 g/100 for buffalograss burs. All seeds were purchased from commercial sources.

Intact burs and legume seeds for each steer were prepared by giving them a light coating of molasses (<500 ml) and mixing them with ca. 1 kg of the standard hay ration. Molasses was used to encourage rapid consumption and prevent burs and seeds from settling to the bottom of the feed bunks where they might not have been consumed. The mixture was fed once in late afternoon about 1 h before normal feeding time, and was always consumed in less than 30 min.

Primed (Hays-treated) 'Texoka' buffalograss burs were fed in the first experiment. The three steers weighed about 300 kg each. They were fed ad lib. and consumed an average of ca. 9.2 kg (air-dry weight) of hay daily. In experiment 2, unprimed Texoka burs were fed to two steers weighing about 425 kg each and to a mature steer weighing about 725 kg. In experiment 3, unprimed 'Cody' buffalograss burs were fed to three steers each weighing about 425 kg. Each steer in the second and third trials was limited to ca. 11.5 kg of hay fed once daily.

Rumen digesta raft concentrations.—Rumens were sampled through the fistulas at 21, 45 and 69 h post feeding. Separate samples of ca. 500 ml of digesta were taken from the top and near the bottom of the floating rumen rafts at each time. These positions were sampled to measure the effects of raft stratification on propagule-type concentrations. Wet sample weights were determined, and buffalograss burs and caryopses, and legume seeds were recovered from the digesta using a dilution and settling method similar to that described

by Ocumpaugh *et al.* (1993). However, rather than drying the residue before seed separation, the remaining residue was placed in a pan of water, and each item visually identified, removed and counted. Concentrations of each propagule type/kg digesta were determined.

Total passage estimates.—Feces from each animal were collected separately for each of four 24-h periods (0–24, 24–48, 48–72, 72–96) beginning immediately after feeding. Each 24-h accumulation from a steer was pooled and thoroughly mixed. Burs, caryopses and legume seeds were recovered from feces samples of known weights. Concentrations of each propagule type were calculated as number/kg feces. Fecal dry-matter percentage was determined after drying to 0% moisture in a forced-air oven at 100 C.

Total fecal output was not measured, but we calculated fecal output and then bur, caryopsis and legume seed passage using the following equations:

$$\text{Total fecal dry weight} = (\text{total feed intake dry weight}) \cdot (1 - \text{feed digestibility})$$

$$\text{Total fecal wet weight} = (1/\text{fecal dry-matter percentage}) \cdot (\text{total fecal dry weight})$$

$$\text{Propagule output} = (\text{propagules/kg wet feces}) \cdot (\text{total fecal wet weight})$$

Estimates for all four periods for each steer and propagule type were summed to arrive at estimates for total passage.

Germination.—Buffalograss burs and caryopses from each steer for each of the 24-h periods were placed in separate 100-mm petri dishes on top of two circles of germination blotter paper. Dishes were placed in a germination chamber with 15 h of light per day. Daytime temperature was 32 C and nighttime temperature was 20 C. Seeds were watered as needed with a tap-water solution containing manganese ethylene bisdithiocarbamate (Maneb) fungicide mixed according to label directions. Germination, defined as emergence of the radicle (Bewley and Black, 1994), was measured for 28 days, once per day for the first 10 days and once every 3 days thereafter. Burs were considered to have germinated after one radicle had emerged, although burs may contain more than one caryopsis.

In addition to percentage germination, mean time to complete germination (MTCG) was calculated with the formula:

$$\text{MTCG} = \sum(t \cdot n) / \sum n$$

where t = time in days from sowing starting at day 0, and n = the number of seeds germinating on that day (Bewley and Black, 1994).

To provide a control treatment, three untreated replications of 100 burs and 100 caryopses from each of the same three seedlots fed were included in each experiment. Caryopses were obtained from the burs by passing them through a Wiley hammermill forage sample grinder (Arthur H. Thomas Co., Philadelphia, Pa.) with a 5 mm screen.

All experiments were conducted as randomized complete block designs, with experiments treated as varietal replications and time periods or sampling times as split plots in time. Each experiment was blocked on steers. Data analysis was by the General Linear Models Procedure and appropriate paired comparisons of least square means at the $P < 0.05$ level (SAS, 1990).

RESULTS AND DISCUSSION

Rumen digesta raft concentrations.—Propagule concentrations were affected by three interactions ($P < 0.05$) (Table 1). In the propagule-type vs. sampling-time interaction, burs initially were numerous but declined significantly at each subsequent sampling time. Caryopses and legume seeds initially were at lower concentrations, but also declined significantly over the entire time. In the propagule-type vs. sampling-position interaction, burs were at significantly higher concentrations than the other propagule types at both positions,

TABLE 1.—Mean rumen-raft concentrations (propagules/kg digesta) for the (1) propagule-type by sampling-time, (2) propagule-type by sampling-position, and (3) sampling-position by sampling-time interactions

Type	H postfeeding			Position	
	21	45	69	Top	Bottom
	Interaction 1			Interaction 2	
Burs	291 Cb ^a	107 Bb	36 Ab	173 Bb	117 Ab
Caryopses	37 Ba	15 ABa	6 Aa	28 Aa	11 Aa
Legumes	30 Ba	3 Aa	3 Aa	14 Aa	10 Aa
	Interaction 3				
Top	142 Cb	54 Bb	19 Aa		
Bottom	97 Ba	30 Aa	11 Aa		

^a Within interactions, means within rows followed by the same uppercase letter, and means within columns followed by the same lowercase letter, are not significantly different at the 0.05 level as determined by paired comparisons

and at higher concentration at the top of the rafts than at the bottom. In the sampling-position vs. sampling-time interaction, total concentrations were significantly higher at the top of the rafts at the first two sampling times, but not at the third.

The primary factor influencing all three interactions was the behavior of the buffalograss burs. Burs persisted longer in the rumen rafts than the other propagule types, and were more common at the top of the rumen rafts than at the bottom. Bur concentrations indicated both delayed passage and a tendency to stratify at the top of the rafts with other larger, lighter particles. Relatively low caryopsis and legume-seed raft concentrations may be explained in at least three ways. First, these propagule types had specific gravities greater than 1.0 and could rapidly settle out of the lighter fibrous material. Although specific gravities of the three propagule types were not determined, caryopses and legume seeds sank immediately when placed in beakers of water to which a drop of dishwashing detergent had been added to reduce surface tension. The burs initially floated, but began to sink after ca. 2 h. Most had sunk by 24 h and all had sunk by 72 h. Second, caryopses and legume seeds are small, well below the 4-mm threshold favored for passage through the reticuloruminal orifice. Burs in our study were near the 4-by-7 mm dimensions reported by Quinn *et al.* (1994), thus making them marginal for passage from the size standpoint alone. Third, caryopses and legume seeds are rounded, smooth objects without structures that would tend to mechanically hold them in the digesta.

In early phases of our study, it was noted that intact burs were difficult to separate from fine fiber in feces or rumen digesta with our wet separation method, which prompted a closer examination of the bur structure. The unique globular structure of the buffalograss bur is crowned by a tuft of three awn-like projections per glume (Hitchcock, 1951; Sutherland, 1986), hereafter referred to simply as awns (Fig. 1a). Microscopic examination of

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FIG. 1a.—Intact buffalograss bur recovered from steer rumen raft, showing digesta adhering to awn-hair complex after vigorous washing. Bar = 2 mm. b. Electron micrograph of hairs found on inner surface of buffalograss awns. Bar = 85 μ m

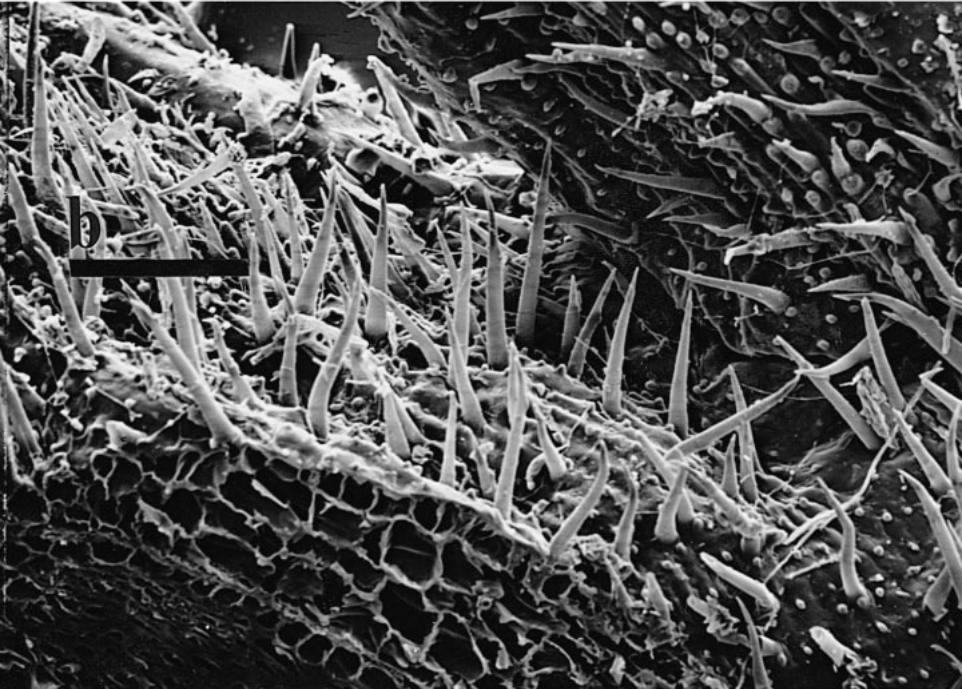
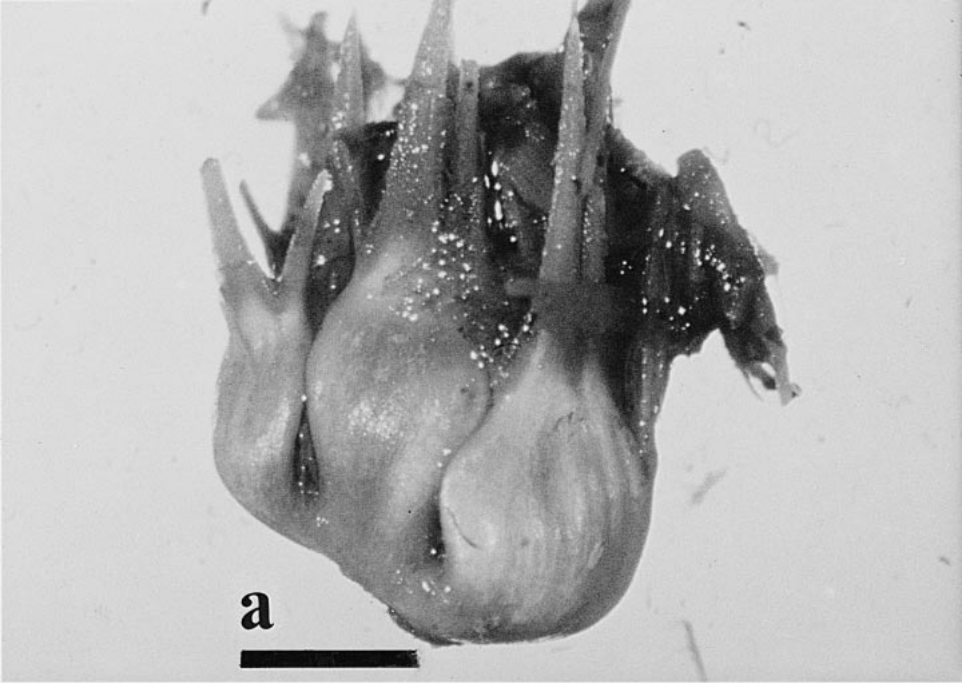


TABLE 2.—Mean numbers of propagules from 30,000 burs and legumes fed passed per steer during each of four 24-h periods postfeeding for the propagule-type by sampling-period interaction, and totals

Type	Period after feeding (h)				Total
	0–24	24–48	48–72	72–96	
	(propagules)				
Burs	153 Aa ^a	483 Aa	272 Aa	89 Aa	998 a
Caryopses	148 Aa	492 Aa	337 Aa	138 Aa	1114 a
Legumes	2830 Bb	5220 Cb	977 Aa	199 Aa	9226 b

^a Means within rows followed by the same uppercase letter, and means within columns followed by the same lowercase letter, are not significantly different at the 0.05 level as determined by paired comparisons

the awns' inner surfaces revealed a dense covering of hairs (Fig. 1b). The hairs are appressed to erect and range in length from about 50 μm to 200 μm. The awn-hair complex was effective in adhering to fine fiber and appeared to hold burs within the rumen raft even after they would otherwise sink. The complex may override any fast-passage effects of a blunt callus as proposed by Thomasson (1985). The burs' tendency to remain within the floating rumen raft delays passage and assures that many of them will be ruminated, increasing the chance that an individual bur eventually will be broken. Low caryopsis concentrations at the first two sampling times also would indicate that the burs are retained intact in the floating rumen raft for an extended time period.

Total passage estimates.—Passage of propagule types was significantly ($P<0.05$) affected by sampling period. The first two sampling periods (Table 2) accounted for the vast majority of legume seeds passed. Passage of legume seeds peaked during period 2, while passage of burs and caryopses was low and statistically uniform ($P>0.05$) across the 4 periods. Total passage of legume seeds also was higher than for the other two propagule types. About 31% of 30,000 legume seeds fed survived passage. The balance presumably were digested, although a few probably remained in the steers at the end of the 4-day collection periods. By comparison, only ca. 3% of burs survived intact. Destruction of burs by remastication is the most likely explanation for the low recovery of intact burs. Retention of the burs in the rumen raft resulted in regurgitation and remastication of a majority of the burs. The relatively low number of caryopses recovered indicated that most of them also were destroyed during passage.

Quinn *et al.* (1994) fed buffalograss burs to yearling Hereford steers, but they did not determine percentage bur survival. However, total passage probably was considerably more than the 3% we found (J.A. Quinn, Department of Biological Sciences, Rutgers University, Piscataway, N.J., pers. comm.). Quinn *et al.* (1994) reported that intact or lightly damaged burs made up 6% to 10% of the feces dry weight from 29 h to 73.25 h post feeding.

Our results for bur survival are not directly comparable to those of Quinn *et al.* (1994) because of the probable effects of differences in feeding methodology. Our steers were fed alfalfa hay and received only a small quantity of molasses with the burs. In addition, we fed only about 30,000 burs compared to 108,000 in their study. Quinn *et al.* (1994) fed their burs with a feed mixture consisting of 90% ground alfalfa, 7% molasses, and 3% cracked corn. Diet has a number of effects on rumen function and the entire digestive system (Church, 1988; Van Soest, 1994). First, the digestibility of our hay was ca. 60%. The digestibility of the diet used during bur feeding in the study by Quinn *et al.* (1994) would have been somewhat higher because of the presence of corn and considerable molasses. This in

turn would reduce fecal dry-matter output as a percentage of the dry matter consumed (Merchen, 1988) and inflate the relative proportion of burs in the feces. Second, the addition of readily fermentable carbohydrates from the corn and molasses would lower rumen pH, from ca. 6.8 for animals on a forage diet to probably less than 6.0 (Owens and Goetsch, 1988). This in turn would increase the water content of material in the entire digestive system, decreasing retention time and feces dry matter content. Lower rumen pH also reduces the extent of rumination (Welch and Hooper, 1988). Finally, the larger volume of burs fed by Quinn *et al.* (1994) may have altered rumen-raft characteristics. With more burs and less forage fiber in the raft, the burs may have settled out of the raft more readily after they were able to sink and escape the rumen without being repeatedly remasticated. In our study, burs remained embedded in the highly fibrous raft after they were able to sink.

Both sets of results are reasonable given the methodologies of the respective studies. It is worth noting, however, that animals consuming buffalograss on rangeland probably would encounter conditions more closely resembling ours. Bur volume consumed per day would be small in proportion to total intake, digestibility of buffalograss would be similar to or less than that of alfalfa hay, depending on season, resulting in greater retention time and increased rumination, and rumen pH would be close to neutral because of the high-fiber diet. Our results suggest percentage bur survival would be low in natural systems.

Most of the burs in our study were destroyed during passage, and relatively few intact caryopses survived passage. It is likely that many caryopses were damaged when the burs were broken and subsequently digested. Others may have survived removal from the burs, but were digested anyway. Free caryopses of buffalograss have no obvious means of protection, such as indurate lemmas and paleas (Hitchcock, 1951; Sutherland, 1986).

If most burs and caryopses are destroyed when consumed by cattle on forage diets, this would initially appear to argue against buffalograss fitting the FF hypothesis, specifically expected trait 7: "Seeds are sufficiently small, tough, hard, and inconspicuous enough to escape the molar mill and spitting response of a large mammal," (Janzen, 1984). However, Janzen (1984) noted that seed mortality is commonly 50% to 99% in endozoochory. He argued that plants typically vastly overproduce seed when compared with the number resulting in new plants, and that high seed mortality is the rule regardless of dispersal means. Furthermore, Janzen suggested in his FF hypothesis that digested seeds are part of the "fruit." Although the mass of buffalograss caryopses in diets of free-ranging animals must be relatively small, the nutrients in those digested, as with other grains, would be nearly all available to the animal (Church, 1988; Van Soest, 1994). Energy costs to the plant, from both consumed foliage and digested seeds, may be the transaction cost the plant pays to participate in the plant-animal interaction (Janzen, 1984).

Germination.—There was a significant ($P < 0.05$) experiment effect in the initial analysis of percentage germination, primarily because of higher germination of primed Texoka fed in experiment 1. Therefore, experiment 1 was analyzed separately, and experiments 2 and 3 were analyzed together. Data for mean time to complete germination were analyzed together because there was no experiment effect.

Percentage germination of burs was negligible in all experiments, but percentage germination of caryopses was significantly higher than for burs recovered from the feces at some time periods (Table 3). In experiment 1, percentage germination of fed caryopses peaked for those recovered during period 1. In experiments 2 and 3, percentage germination of fed caryopses peaked for those recovered during periods 2 and 3.

It should be noted, however, that the burs were kept in the germination chamber after the 28-day run. Some continued to germinate, although numbers and days were not recorded. Quinn *et al.* (1994) reported higher germination percentages during 12 wk for

TABLE 3.—Mean percentage germination after 28 days of buffalograss burs and caryopses from the control treatment and those recovered from the feces during four 24-h periods postfeeding

Type	Control ^a	Period after feeding (h)			
		0–24	24–48	48–72	72–96
(%)					
Experiment 1					
Burs	7.3 Aa ^b	0 Aa	0 Aa	1.3 Aa	0 Aa
Caryopses	82.7 Cb	21.8 Bb	9.0 Ab	4.9 Aa	2.7 Aa
Experiments 2 and 3					
Burs	0.5 Aa	0.8 Aa	1.5 Aa	3.0 Aa	3.7 Aa
Caryopses	28.8 Cb	2.1 Aa	9.4 ABb	12.2 Bb	4.4 Aa

^a Control treatment was germination of burs and caryopses that had not been fed
^b Means within rows followed by the same uppercase letter, and within experiment groups, means within columns followed by the same lowercase letter, are not significantly different at the 0.05 level as determined by paired comparisons

cattle-treated burs planted in soil or soil plus manure, with time required for 50% of the burs to germinate ranging from ca. 40 d to 80 days. Had our study employed methods more similar to those of Quinn *et al.* (1994) our germination levels may have been much closer to their results.

Percentage germination of caryopses recovered from the feces likely would have been much higher if it had been possible to identify only truly viable caryopses. All fed caryopses lacking obvious mechanical damage and having a bright tan color were recovered from the feces samples, counted and set to germinate. However, many of them rotted, indicating they had damage not visible to the eye. Had it been possible to recover only viable caryopses the percentage germinating would have been higher.

Mean time to complete germination was not different for burs and caryopses in the control treatment, but was considerably less ($P < 0.05$) for caryopses than for burs in all fed treatments (Table 4). There were no differences among time periods for caryopses recovered from the feces, but MTCG was significantly less for the control treatment among burs.

Even considering the number of damaged caryopses included in the samples, free cary-

TABLE 4.—Mean time in days to complete germination in 28-day runs for buffalograss burs and caryopses from the control treatment and those recovered from the feces during 4 24-h periods post-feeding

Type	Control ^a	Period			
		1	2	3	4
		(d)			
Burs	7.6 Aa ^b	25.2 Bb	23.1 Bb	19.2 Bb	21.8 Bb
Caryopses	4.1 Aa	6.5 Aa	7.9 Aa	4.7 Aa	5.6 Aa

^a Control treatment was germination of burs and caryopses that had not been fed
^b Means within rows followed by the same uppercase letter, and means within columns followed by the same lowercase letter, are not significantly different at the 0.05 level by paired comparisons

opses germinated at higher percentages over the 28-day germination period and much sooner than intact burs after feeding.

Intact buffalograss burs exhibit low and slow germination, which at times may be advantageous in that seeds are able to avoid unfavorable periods, for example dry or cold weather, and germinate when conditions are favorable (Bewley and Black, 1994). The fact that buffalograss bur germination is improved by soaking may be evidence of a dormancy-breaking mechanism, common in arid-region plants, that is triggered by adequate moisture. Buffalograss appears to have a more flexible strategy whereby seeds are provided with a range of dormancy levels, so that at least some are prepared to germinate at any time after dispersal when conditions of temperature and moisture are favorable (Bewley and Black, 1994). To a limited extent, burs from both a wild population and a cultivar showed differential germinability of seeds within burs in response to three separated month-long periods of favorable moisture (Quinn and Engle, 1986). Specifically, 33% of the burs from the wild population produced seedlings in more than one of the periods separated by simulated drought in which all seedlings died. Ingestion enhances this differential germinability by release of some caryopses from the burs when they are masticated (Svoboda, 1991), and by internal soaking of burs that remain intact (Wenger, 1941; Fry *et al.*, 1993). In its association with grazing ruminants, buffalograss appears to have a highly developed strategy whereby seeds are provided with a wide range of dormancy levels, allowing them to respond to favorable conditions over an extended time.

The results for rumen-propagule concentrations and fecal passage suggest that the awn-hair complex delays passage through the animal. This would provide dispersal at greater distances than otherwise when buffalograss burs are consumed by free-ranging grazers. It also is possible that the complex increases external transport by animals when the complex adheres to pelts, which is not mutually exclusive with any role in endozoochory. Ridley (1930) listed numerous species of forb and grass seed recovered from the woolly pelts of both bison and sheep. Bison, with their tendency to wallow, would be good candidates for external as well as internal transport of buffalograss.

Although relatively few free caryopses survive passage, as a proportion of those consumed, their potential contribution to reproductive success should not be dismissed. As Janzen (1984) noted in proposing the FF hypothesis, a high percentage of seed survival is not a requirement. The important points are that some seeds survive, that they be dispersed, and have a chance of being deposited in a favorable location.

Our results support the conclusion of Quinn *et al.* (1994) that buffalograss is an excellent fit for the FF hypothesis. The results also suggest that the plant/animal interaction is more complex and highly evolved than it initially appeared to be, with buffalograss possessing adaptations to the ruminant digestive system to increase dispersal distance and provide greater germination flexibility.

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LITERATURE CITED

- AHRING, R. M. AND G. W. TODD. 1977. The bur enclosure of the caryopses of buffalograss as a factor affecting germination. *Agron. J.*, 69:15–17.

- BEWLEY, J. D. AND M. BLACK. 1994. Seeds: physiology of development and germination, 2nd ed. Plenum Press, New York, N.Y. 445 p.
- BURTON, G. W. AND J. S. ANDREWS. 1948. Recovery and viability of seeds of certain southern grasses and lespedeza passed through the bovine digestive tract. *J. Agric. Res.*, **76**:95–103.
- CHURCH, D. C. (ED.). 1988. The ruminant animal: digestive physiology and nutrition. Prentice-Hall, Englewood Cliffs, N.J. 564 p.
- DORE, W. G. AND L. C. RAYMOND. 1942. Pasture studies XXIV: Viable seeds in pasture soil and manure. *Sci. Agric.*, **23**:69–79.
- FRY, J., W. UPHAM AND L. LEUTHOLD. 1993. Seeding month and seed soaking affect buffalograss establishment. *Hortic. Sci.*, **28**:902–903.
- HARMON, G. W. AND F. D. KEIM. 1934. The percentage and viability of weed seeds recovered in the feces of farm animals and their longevity when buried in manure. *Am. Soc. Agron. J.*, **26**:762–767.
- HITCHCOCK, A. S. 1951. Manual of grasses of the United States. Revised by Agnes Chase. *U.S. Dep. Agric. Misc. Public.* **200**. Washington, D.C. 1051 p.
- HOFMANN, R. R. 1988. Anatomy of the gastro-intestinal tract. p. 145–171. *In*: D. C. Church (ed.). The ruminant animal: digestive physiology and nutrition. Prentice-Hall, Englewood Cliffs, N.J.
- JANZEN, D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.*, **123**:338–353.
- LYFORD, S. L. 1988. Growth and development of the ruminant digestive system, p. 44–63. *In*: D. C. Church (ed.). The ruminant animal: digestive physiology and nutrition. Prentice-Hall, Englewood Cliffs, N.J.
- MERCHEN, N. R. 1988. Digestion, absorption and excretion in ruminants, p. 172–201. *In*: D. C. Church (ed.). The ruminant animal: digestive physiology and nutrition. Prentice-Hall, Englewood Cliffs, N.J.
- OCUMPAUGH, W. R., J. W. STUTH AND S. R. ARCHER. 1993. Recovery and germination of switchgrass seed fed to cattle, p. 318–319. *In*: Proceedings of the XVII International Grassland Congress. Keeling & Mundy, Ltd., Palmerston North, New Zealand.
- OWENS, F. N. AND A. L. GOETSCH. 1988. Ruminal fermentation, p. 145–171. *In*: D. C. Church (ed.). The ruminant animal: digestive physiology and nutrition. Prentice-Hall, Englewood Cliffs, N.J.
- QUINN, J. A. AND J. L. ENGEL. 1986. Life-history strategies and sex ratios for a cultivar and a wild population of *Buchloe dactyloides* (Gramineae). *Am. J. Bot.*, **73**:874–881.
- , D. P. MOWREY, S. M. EMANUELE AND R. D. B. WHALLEY. 1994. The “foliage is the fruit” hypothesis: *Buchloe dactyloides* (Poaceae). *Am. J. Bot.*, **81**:1545–1554.
- RIDLEY, H. N. 1930. The dispersal of plants throughout the world. L. Reeve & Co., Ltd., Ashford, Kent, Great Britain. 744 p.
- SIMAO NETO, M., R. M. JONES AND D. RATCLIFF. 1987. Recovery of pasture seed ingested by ruminants. 1. Seed of six tropical pasture species fed to cattle, sheep and goats. *Aust. J. Exp. Agric.*, **27**: 239–246.
- SAS INSTITUTE, INC. 1990. SAS/STAT user's guide: statistics, version 6, 4th ed. SAS Institute, Inc., Cary, N.C. 1686 p.
- SUTHERLAND, D. 1986. *Poaceae*, p. 1148. *In*: T. M. Barkley (ed.). Flora of the Great Plains. University of Kansas Press, Lawrence.
- SVOBODA, J. F. 1991. Seedling germination and establishment of buffalograss caryopses vs. burs. M.S. Thesis, University of Nebraska-Lincoln, Lincoln. 96 p.
- THOMASSON, J. R. 1985. Miocene fossil grasses: possible adaptation in reproductive bracts (lemma and palea). *Ann. Mo. Bot. Gard.*, **72**:843–851.
- VAN SOEST, P. J. 1994. Nutritional ecology of the ruminant, 2nd ed. Comstock Publishing Associates, Cornell University Press, Ithaca, N.Y. 476 p.
- WELCH J. G. AND A. P. HOOPER. 1988. Ingestion of feed and water, p. 108–116. *In*: D. C. Church (ed.). The ruminant animal: digestive physiology and nutrition. Prentice-Hall, Englewood Cliffs, N.J.

- WENGER, L. E. 1941. Soaking buffalograss (*Buchloe dactyloides*) seed to improve its germination. *J. Am. Soc. Agron.*, **33**:135–141.
- WICKLOW, D. T. AND J. C. ZAK. 1983. Viable grass seeds in herbivore dung from a semi-arid grassland. *Grass Forage Sci.*, **38**:25–26.

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